

# A comparative study of morphometry in shell-bearing molluscs

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## Abstract

A comparative study was conducted on the ontogenetic variation in morphometry of a total of 29 shell-bearing molluscan species occurring on an intertidal stony shore in south-western Japan. The relationships between shell size and total weight and between shell size and flesh weight were all highly significant on logarithmic scales with the slopes having values of about three. The arcsine-transformed proportion of shell weight out of total weight varied among and within different morphological/taxonomic groups, ranging from 58.6% in *Acanthochiton defilippi* to 76.4% in *Nerita albicilla*. The allometry of shell weight was analysed by regressing the arcsine transformed values of the proportion of shell weight against total weight in each species. The slope ( $\beta$ ) of the regression varied substantially among different taxa, with all three possible cases, i.e.  $\beta > 0$ ,  $\beta \approx 0$  and  $\beta < 0$ , being observed. Thus, depending on molluscan species, the proportion of shell mass either (1) increases, (2) does not change, or (3) decreases with increasing body mass. Variation in the value of  $\beta$  was to some extent explained by the proportion of shell mass of young individuals of each species; species with relatively high proportions of shell mass in small individuals tended to have low  $\beta$ . Interspecifically, it was shown that shell mass scaled in proportion to body mass for this assemblage of 29 species. Consideration was given to the theoretical background of variation in shell morphometry, with particular reference to the shell as a defence structure.

**Key words:** molluscs, allometry, shell, defence, interspecific differences

## INTRODUCTION

Amongst marine taxa, molluscs have achieved notable evolutionary divergence over the Phanerozoic and acquired a unique variety of morphologies (Sepkoski, 1981; Russell-Hunter, 1983; Runnegar & Pojeta, 1985). In particular, the evolution of a hard outer skeleton (shell) has been associated with a great divergence of morphologies in this group. While shell is useful as an effective means of protection against predators and physical damage to the internal tissues (Stanley, 1970, 1988; Vermeij, 1977; Raffaelli, 1982; Kardon, 1998), its production can be costly and may place certain limits on the growth of an individual (Currey, 1988). Calcium carbonate is a major component of molluscan shells and is available in abundance in marine environments, but other components, particularly protein, are metabolically costly to produce (Palmer, 1983). Further, possession of large or heavy shells generally means that the speed of movement and manoeuvrability of the animal are restricted to various degrees. Thus, molluscs must have had to weigh the costs and benefits of shell production through evolutionary time.

As molluscan size varies both intra- and interspecifically, the relative investment into shell and non-shell parts can change ontogenetically and within/between species. Such variability is likely to reflect changing ecophysiological requirements and constraints with body size, alongside genetic and environmental influences on shell morphology (Currey & Hughes, 1982; Palmer, 1990; Boulding & Hay, 1993; Boulding & van Alstyne, 1993). Analyses of allometric relationships have been successful in generating a host of important insights into basic ecophysiological characteristics of organisms, particularly vertebrates (Schmidt-Nielsen, 1975, 1984). However, there is a paucity of comparative studies on the allometric relations among aquatic invertebrates including molluscs. The present study deals with an entire assemblage of molluscs occurring in the same habitat to make a comparative analysis of morphometry. The molluscan assemblage of a stony shore in Amakusa, south-western Japan, includes a total of 29 common shell-bearing species of gastropods and bivalves. As these species experience similar environmental conditions, extrinsic factors which are known to affect the shell morphology of some species

(e.g. degree of exposure to waves) are effectively excluded. This is considered an advantage for a comparative study involving different taxa.

The aim of the present study was to compare the size-related morphometric characteristics, particularly of shells, among a set of molluscan taxa and to demonstrate the variability of allometric relations. Attention has been drawn to the proportion that shell mass has out of total body mass in different molluscan species occurring on the same shore. Based on the documentation and analysis of allometric patterns, consideration is given to the possible causes of variability among species.

## MATERIALS AND METHODS

### Sample processing

Samples of molluscs were collected from the stony shore of Magarizaki in the Amakusa Shimoshima island (32°32'N, 130°02'E), south-western Japan, in summer–autumn 1998. The environmental conditions of this sampling site were described in detail by Takada & Kikuchi (1990). For each of 29 species, individuals of different sizes were collected by hand and placed in plastic bags for immediate transport to the laboratory. Although an attempt was made to gather a minimum of 70 individuals for each species, some species were relatively scarce and the target number could not be achieved for 3 species. Nevertheless, an average of 115 individuals per species was sampled and subjected to morphometric analysis. On return to the laboratory, the shell size of each individual was measured to the nearest 0.01 mm with vernier callipers. Shell size referred to shell height in carnivorous neogastropods, shell width in herbivorous non-limpet gastropods, shell length in limpets and bivalves, and the width of the fifth plate in chitons. After shell measurements were taken, samples were dried at 60 °C for 72 h to obtain total dry weight ( $W_t$ ). These samples were further dried at 500 °C for 3–4 h to incinerate soft parts and obtain shell weight ( $W_s$ ). Note that this measure of shell weight refers mainly to the calcium carbonate parts, as proteins and other organic parts were removed through incineration. Dry weight of the soft body parts (tissue weight,  $W_f$ , including the proteinous fraction of the shell) was derived as the difference between total dry weight and shell weight ( $W_f = W_t - W_s$ ).

In order to facilitate comparisons, molluscan species were classified into 5 categories based on morphological similarities: (1) 'whelks' or carnivorous neogastropods including *Japeuthria ferrea*, *J. cingulata*, *Thais clavigera*, *Morula musiva* and *Ergalatax contractus*; (2) 'snails' or herbivorous non-limpet gastropods including *Monodonta labio*, *M. perplexa*, *Lunella coronata*, *Chlorostoma xanthostigma*, *C. lischkei*, *Littorina brevicula*, *Granulittorina exigua*, *Nerita japonica* and *N. albicilla*; (3) 'limpets' including *Nipponacmea concinna*, *N. teramachii*, *N. nigrans*, *N. fuscoviridis*, *N. schrenckii* and *Patelloida pygmaea*; (4) 'chitons' including *Acantho-*

*chiton defilippi*, *Liolophura japonica*, *Ischnochiton comptus*; (5) 'bivalves' including *Ruditapes variegatus*, *Septifer virgatus*, *S. bilocularis*, *Barbatia virescens* and *Cardita leana*.

### Data analysis

Analysis of allometric relationship was carried out with reference to a basic equation  $Y = AX^B$  (Schmidt-Nielsen, 1984).  $B$  is of interest as it is the allometric exponent or the slope of the log-transformed regression line of the above equation. When  $X$  is taken as a body size variable,  $B \approx 1$  will indicate size proportionality in variable  $Y$ ,  $B = 0$  will indicate that variable  $Y$  is independent of size, while  $B > < 1$  will indicate allometry.

In each species, total weight ( $W_t$ ) and tissue weight ( $W_f$ ) were related to shell size ( $L$ ) as:

$$W_t = a L^b \quad \text{or} \quad \log W_t = \log a + b \log L \quad (1)$$

$$W_f = c L^d \quad \text{or} \quad \log W_f = \log c + d \log L \quad (2)$$

where  $\log a$  and  $\log c$  are the intercept parameters and  $b$  and  $d$  are the slope parameters. The allometry of shell weight was further analysed by regressing the arcsine transformed values of the proportion of shell weight ( $P_s = (W_s/W_t) \times 100$ ) against total weight in the form of:

$$\text{arcsine } P_s = \alpha + \beta \log W_t \quad (3)$$

where  $\alpha$  is a constant (intercept) and  $\beta$  is the slope of the regression. This regression has an advantage of allowing variation in the proportion of shell weight to be expressed as a function of total mass within a species. In addition, variation in  $\beta$  among molluscan taxa was analysed further by plotting  $\beta$  against mean percentage shell weight of the lowest quartile of individuals (i.e. small individuals (in terms of total weight) constituting 25% of all in each species). This is based on a hypothesis that the degree of change in the proportion of shell weight with increasing total mass is a developmental phenomenon which is partly dictated by the initial proportion of shell weight in small individuals.

Further, in order to examine the overall relationship between shell weight and total weight, the former was regressed against the latter on logarithmic scales, thus,

$$\log W_s = g + h \log W_t \quad (4)$$

where  $g$  is the intercept parameter and  $h$  is the slope parameter.

## RESULTS

Regressions of total weight on shell size (eqn 1) and tissue weight on shell size (eqn 2) were both highly significant for all species with the coefficient of determination ( $r^2$ )  $> 0.93$  for total weight and 0.86 for tissue weight (Table 1). The allometric exponent  $b$  ranged from 2.71 to 3.51 with a mean of 3.10 and  $d$  ranged from 2.60 to 3.38 with a mean of 3.0. When the entire data set was taken into consideration, the numbers of

**Table 1.** Parameter values of the regressions log total weight on log shell size ( $\log W_t = a + b \log L$ ) and log flesh weight on log shell size ( $\log W_f = c + d \log L$ ), with coefficients of determination ( $r^2$ ).  $n$ , sample size

Species	$n$	$a$	$b$	$r^2$	$c$	$d$	$r^2$
<b>Whelks</b>							
<i>Japeuthria ferrea</i>	168	-3.83	2.71	0.99	-4.73	2.78	0.99
<i>J. cingulata</i>	168	-4.24	3.20	0.99	-5.30	3.31	0.98
<i>Thais clavigera</i>	96	-3.54	2.77	0.98	-4.90	2.97	0.94
<i>Ergalatax contractus</i>	98	-3.85	2.81	0.98	-5.10	2.99	0.92
<i>Morula musiva</i>	96	-4.43	3.51	0.95	-5.38	3.38	0.90
<b>Snails</b>							
<i>Lunella coronata</i>	116	-3.53	3.00	1.00	-4.90	3.32	0.99
<i>Monodonta labio</i>	153	-3.69	3.19	0.99	-4.76	3.23	0.99
<i>M. perplexa</i>	163	-3.51	2.88	1.00	-4.14	2.61	0.96
<i>Chlorostoma xanthostigma</i>	87	-3.65	3.08	1.00	-4.72	3.11	0.99
<i>C. lischkei</i>	77	-3.91	3.32	1.00	-4.59	3.11	0.99
<i>Nerita japonica</i>	134	-3.49	2.84	1.00	-4.31	2.60	0.98
<i>N. albicilla</i>	29	-3.98	3.29	0.97	-4.90	3.03	0.97
<i>Littorina brevicula</i>	138	-3.43	3.02	0.99	-4.83	3.28	0.97
<i>Granulilittorina exigua</i>	204	-4.00	3.44	0.98	-4.42	2.67	0.94
<b>Limpets</b>							
<i>Nipponacmea teramachii</i>	170	-4.34	2.97	0.98	-4.97	2.86	0.91
<i>N. schrenckii</i>	109	-4.67	3.03	0.99	-5.27	2.91	0.94
<i>N. concinna</i>	103	-4.76	3.36	0.96	-5.04	2.85	0.93
<i>N. nigrans</i>	127	-4.51	3.19	0.94	-5.38	3.23	0.92
<i>N. fuscoviridis</i>	115	-4.73	3.34	0.97	-5.02	2.93	0.86
<i>Patelloida pygmaea</i>	293	-4.39	3.25	0.93	-4.69	2.68	0.86
<b>Chitons</b>							
<i>Acanthochiton defilippi</i>	106	-2.49	3.14	0.93	-3.12	3.25	0.90
<i>Liolophura japonica</i>	70	-3.26	3.07	0.99	-3.88	3.03	0.97
<i>Lepidozonia coreanica</i>	33	-3.83	3.35	0.98	-4.14	2.87	0.98
<i>Ischnochiton comptus</i>	98	-3.85	3.35	0.97	-4.20	2.96	0.94
<b>Bivalves</b>							
<i>Barbatia virescens</i>	57	-4.12	2.95	0.98	-5.09	3.09	0.97
<i>Cardita leana</i>	76	-3.72	2.92	0.98	-4.93	3.09	0.92
<i>Septifer bilocularis</i>	99	-3.91	2.93	0.99	-4.75	2.95	0.96
<i>S. virgatus</i>	53	-4.06	2.98	0.99	-4.78	2.95	0.98
<i>Ruditapes variegatus</i>	102	-4.20	3.11	0.99	-5.11	2.98	0.98

these exponents  $< 3.0$  and of those  $> 3.0$  were comparable and no significant bias towards either small or large values (with reference to 3.0) was detected (binomial test,  $P > 0.05$ ).

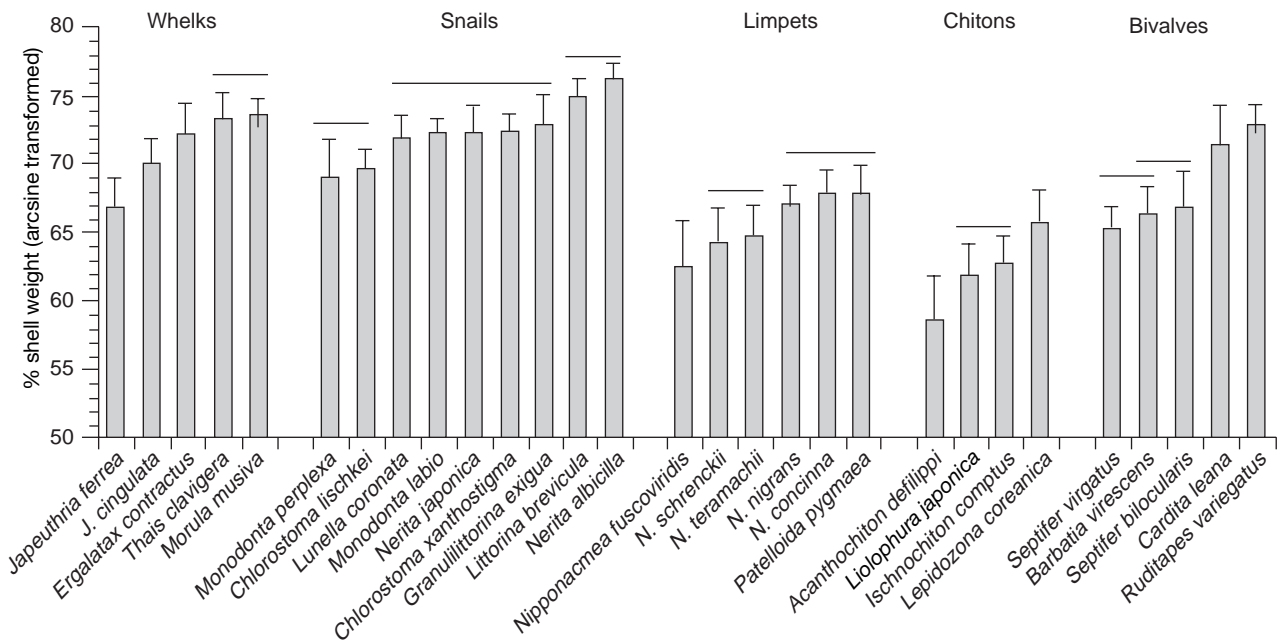
The proportion (arcsine transformed) of shell weight out of total weight varied substantially among molluscan species, ranging from 58.6% in *Acanthochiton defilippi* to 76.4% in *Nerita albicilla* (Fig. 1). Of the five morphological groups, snails and whelks had relatively high proportions of shell weight (mean proportion values: snails, 72.5%; whelks, 71.2%), while limpets and chitons had lower proportions (65.8 and 62.3%, respectively). Bivalves had intermediate values (mean of 68.6%). Within each group, the proportion of shell weight varied significantly (Scheffé's  $F$  test on arcsine transformed values,  $P < 0.05$ ) and three to four sub-groups of similar shell proportions were recognizable. In each group species which inhabit upper zones of the intertidal tended to have higher proportions of shell weight than other taxa (though there were some exceptions). Of the whelks, *Morula musiva* and *Thais clavigera* had relatively high values (73.6 and 73.4%, respectively), while values were low for *Japeuthria ferrea* (66.9%) and *J. cingulata* (70.0%). The snails *Nerita*

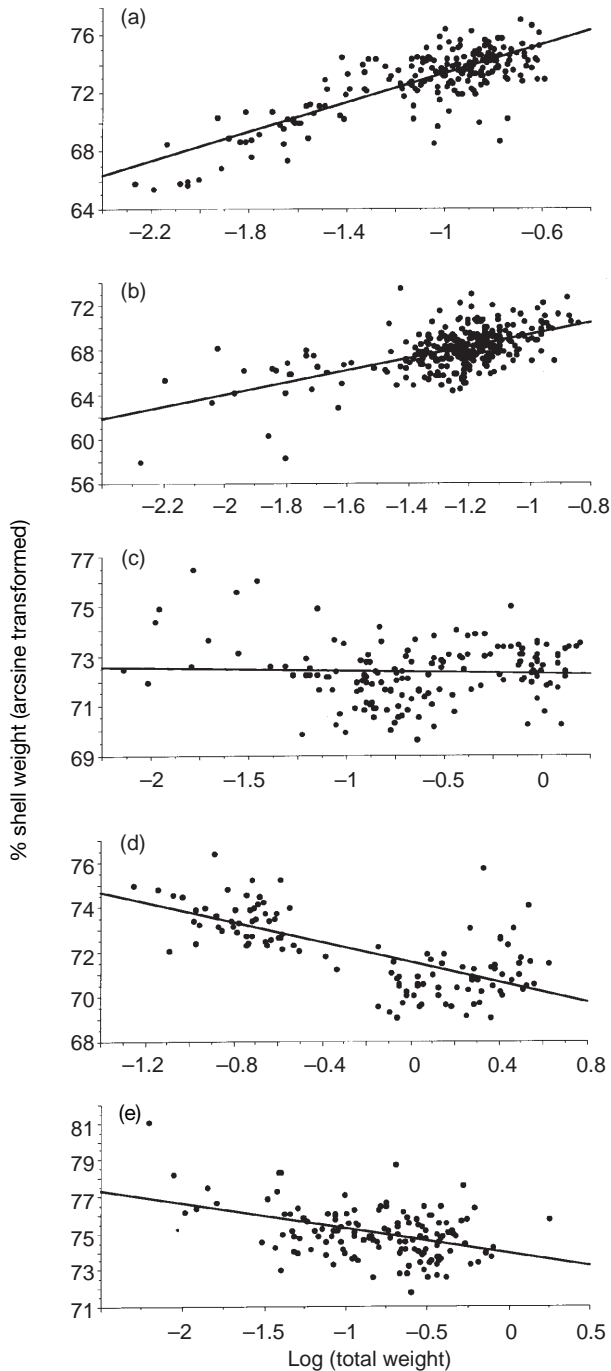
*albicilla* (76.4%) and *Littorina brevicula* (75.0%) had particularly high proportions of shell weight, but other species had lower values. Of the limpets, *Patelloida pygmaea*, *Nipponacmea concinna* and *N. nigrans* had higher proportions of shell weight than others. Bivalves showed a relatively large variation in the proportion of shell weight, ranging from 65.3% in *Septifer virgatus* to 73.1% in *Ruditapes*. Chitons as a group had low values in the range 58.7–65.8%.

In the regression of the arcsine transformed values of the proportion of shell weight ( $P_s = (W_s/W_t) \times 100$ ) against total weight ( $W_t$ ) (eqn 3), the coefficient of determination  $r^2$  ranged from 0.002 to 0.678 with 20 out of 29 species showing statistical significance ( $P < 0.05$ ) (Table 2). Further, Bonferroni's correction was applied to the probability calculation so that more stringent criteria were employed for the assessment of significance; this resulted in 12 out of 29 species showing a significant regression. However, notably among the significant regressions both positive and negative values of the slope  $\beta$  occurred, indicating that the proportion of shell weight increased with body size in some taxa, while in others it decreased. Thus, three distinct patterns for shell weight allometry were recognizable in this

**Table 2.** Parameter values of the regression log total weight on arcsine transformed proportion of shell weight,  $\text{arc}P_s = \alpha + \beta \log W_t$ ;  $n$ , sample size;  $r^2$ , coefficient of determination. NS,  $P > 0.05$ ; \*\*significant at  $P < 0.01$  after Bonferroni's correction

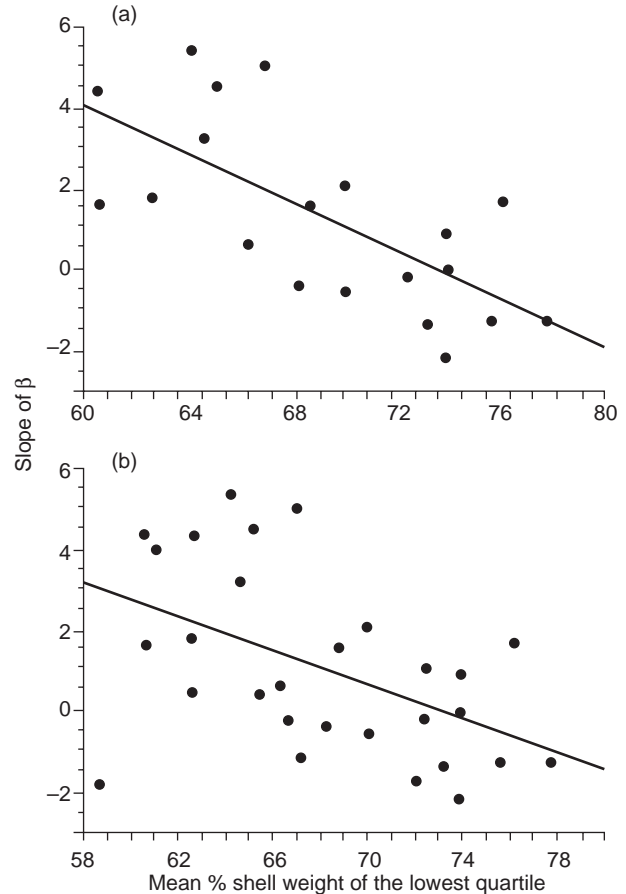
Species	$n$	$\alpha$	$\beta$	$r^2$	$P$
<b>Whelks</b>					
<i>Japeuthria ferrea</i>	168	66.7	-0.463	0.017	NS
<i>J. cingulata</i>	168	69.9	-0.607	0.031	0.023
<i>Thais clavigera</i>	96	73.4	-1.323	0.080	0.0053
<i>Ergalatax contractus</i>	98	71.7	-1.434	0.056	0.0192
<i>Morula musiva</i>	96	73.8	0.849	0.032	NS
<b>Snails</b>					
<i>Lunella coronata</i>	116	71.6	-2.209	0.469	< 0.0001**
<i>Monodonta labio</i>	153	72.3	-0.108	0.002	NS
<i>M. perplexa</i>	163	70.9	3.206	0.275	< 0.0001**
<i>Chlorostoma xanthostigma</i>	87	72.5	-0.228	0.014	NS
<i>C. lischkei</i>	77	70.0	1.524	0.307	< 0.0001**
<i>Nerita japonica</i>	134	73.9	2.029	0.337	< 0.0001**
<i>N. albicilla</i>	29	76.1	1.600	0.187	0.0191
<i>Littorina brevicula</i>	138	74.0	-1.332	0.178	< 0.0001**
<i>Granulilittorina exigua</i>	204	78.3	4.991	0.636	< 0.0001**
<b>Limpets</b>					
<i>Nipponacmea teramachii</i>	170	67.3	1.786	0.034	0.0165
<i>N. schrenckii</i>	109	66.4	1.599	0.059	0.0109
<i>N. concinna</i>	103	72.1	4.499	0.381	< 0.0001**
<i>N. nigrans</i>	127	67.9	0.573	0.005	NS
<i>N. fuscoviridis</i>	115	69.4	4.353	0.126	< 0.0001**
<i>Patelloida pygmaea</i>	293	74.7	5.369	0.336	< 0.0001**
<b>Chitons</b>					
<i>Acanthochiton defilippi</i>	106	57.6	-1.746	0.076	0.0041
<i>Liolophura japonica</i>	70	61.9	0.437	0.014	NS
<i>Lepidozona coreanica</i>	33	68.1	4.330	0.678	< 0.0001**
<i>Ischnochiton comptus</i>	98	67.0	4.003	0.378	< 0.0001**
<b>Bivalves</b>					
<i>Barbatia virescens</i>	57	65.8	-1.194	0.047	NS
<i>Cardita leana</i>	76	71.2	-1.769	0.086	0.0103
<i>Septifer bilocularis</i>	99	66.8	-0.242	0.003	NS
<i>S. virgatus</i>	53	65.6	0.385	0.022	NS
<i>Ruditapes variegatus</i>	102	73.5	0.968	0.116	0.0003**

**Fig. 1.** Proportions of shell weight out of total weight in different molluscan taxa. Horizontal lines in each taxonomic group indicate values which are not significantly different (Scheffé's  $F$  test on arcsine transformed values,  $P < 0.05$ ).



**Fig. 2.** Relationship between proportion of shell weight (arcsine-transformed percentage values,  $\text{arc}P_s$ ) and log total weight. (a) *Granulittorina exigua*,  $\text{arc}P_s = 78.3 + 4.99 \log W_t$ ,  $r^2 = 0.63$ ; (b) *Patelloida pygmaea*,  $\text{arc}P_s = 74.7 + 5.37 \log W_t$ ,  $r^2 = 0.34$ ; (c) *Monodonta labio*,  $\text{arc}P_s = 72.3 - 0.108 \log W_t$ ,  $r^2 = 0.002$ ; (d) *Lunella coronata*,  $\text{arc}P_s = 71.6 - 2.21 \log W_t$ ,  $r^2 = 0.47$ ; (e) *Littorina brevicula*,  $\text{arc}P_s = 74.0 - 1.33 \log W_t$ ,  $r^2 = 0.18$ .

molluscan assemblage: (1) an increasing proportion of shell mass with body size (i.e.  $\beta > 0$ ), e.g. *Granulittorina exigua* and *Patelloida pygmaea* (Fig. 2a, b); (2) no change in the proportion of shell mass with body size ( $\beta \approx 0$ ), e.g. *Monodonta labio* (Fig. 2c); (3) a decreasing



**Fig. 3.** Relationship between slope  $\beta$  in  $\log W_t - \text{arc}P_s$  regression and mean percentage shell weight of the lowest quartile of individuals for: (a) snails, whelks and limpets ( $y = 22.1 - 0.301x$ ,  $r^2 = 0.48$ ); (b) all taxa ( $y = 15.5 - 0.213x$ ,  $r^2 = 0.25$ ).

proportion of shell mass with body size ( $\beta < 0$ ), e.g. *Lunella coronata* and *Littorina brevicula* (Fig. 2d, e). There were more taxa which had increasing proportions of shell mass than those having decreasing proportions, while other taxa showed no change. For the absolute magnitude of  $\beta$ , positive values of  $\beta$  tended to have a larger magnitude (many of them  $> 2.0$ ) than negative values. Amongst five morphological groups, it is notable that whelks generally had negative values of  $\beta$ , while limpets had positive values (Table 2).

The results of regressing  $\beta$  against mean percentage shell weight of the lowest quartile of individuals showed that the slope  $\beta$  had a significant ( $P < 0.01$ ) negative relationship with the proportion of shell weight of small individuals (Fig. 3). Thus, nearly half (48%) of the variation in  $\beta$  was explained by variation in percentage shell weight of small individuals in the case of whelks, snails and limpets (Fig. 3a) and a quarter of variation was explained for all the molluscan taxa combined (Fig. 3b). Further, the slope  $\beta$  was significantly related to the slope  $b$ , though the tendency was weak when only whelks, snails and limpets were considered ( $P = 0.053$  for whelks, snails and limpets and  $P = 0.0033$  for all taxa).

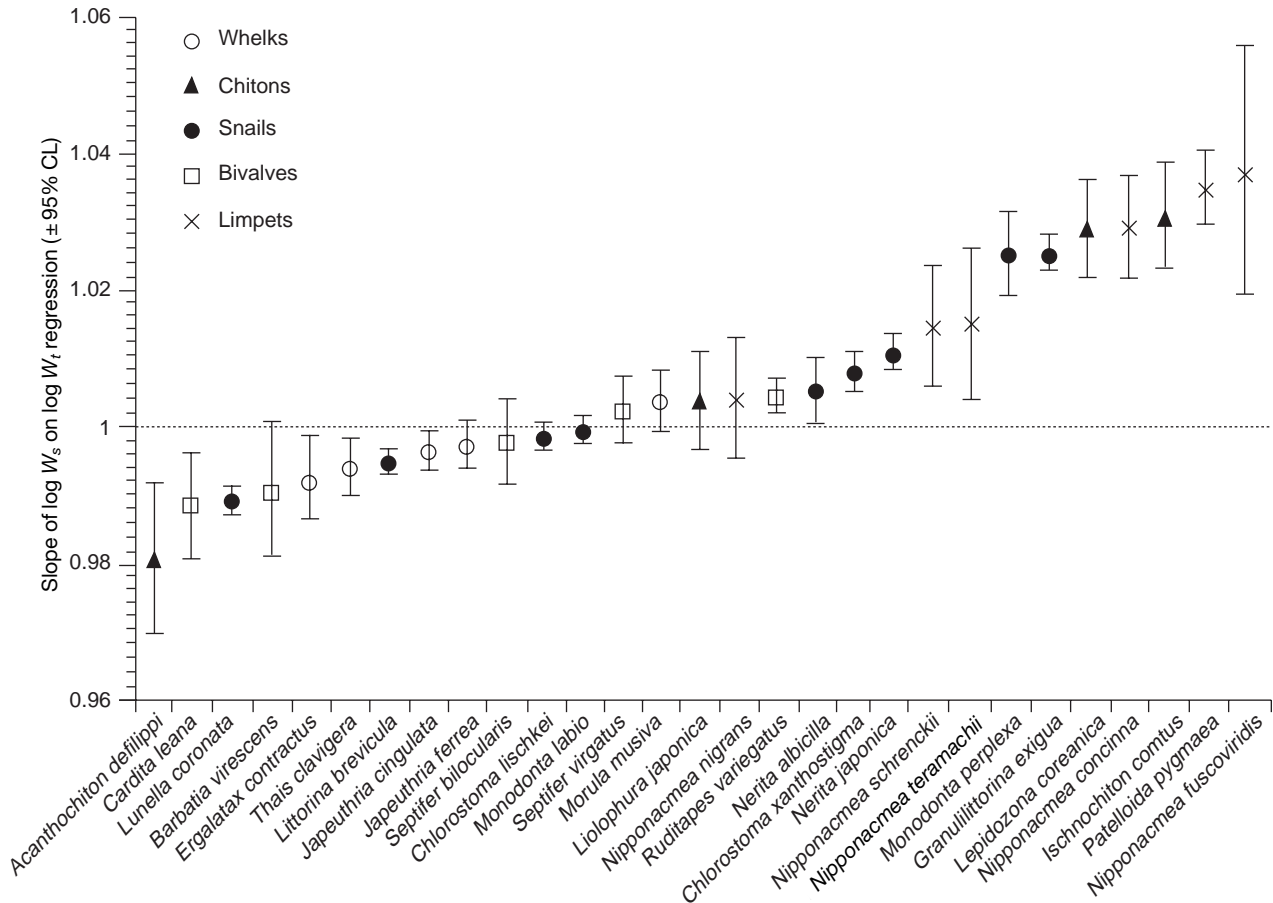


Fig. 4. Slopes of log shell weight on log total weight regression arranged in increasing order for 29 molluscan taxa.

When shell weight was regressed against total weight on logarithmic scales (eqn 4), the slope  $h$  varied within a narrow range around 1, from  $h = 0.981$  in *A. defilippi* to 1.038 in *N. fuscoviridis* (Fig. 4). Seven species with relatively high values of  $h$  (*N. fuscoviridis* to *M. perplexa*) were those which demonstrated high values of  $\beta$ . No species of whelks and bivalves had values of  $h$  significantly  $> 1.0$ . Overall, the relative values of  $h$  corresponded with those of  $\beta$  in the previous regression, as expected from mathematical similarity between the two relationships.

Finally, the interspecific relationship between total weight and shell weight was investigated by plotting the mean shell weight and mean total weight of 10 largest individuals of each species (Fig. 5). The 29 species demonstrated an almost perfect fit of a regression line with the slope nearly equal to unity, suggesting that shell mass scales in proportion to body mass when molluscan taxa of different sizes are considered together.

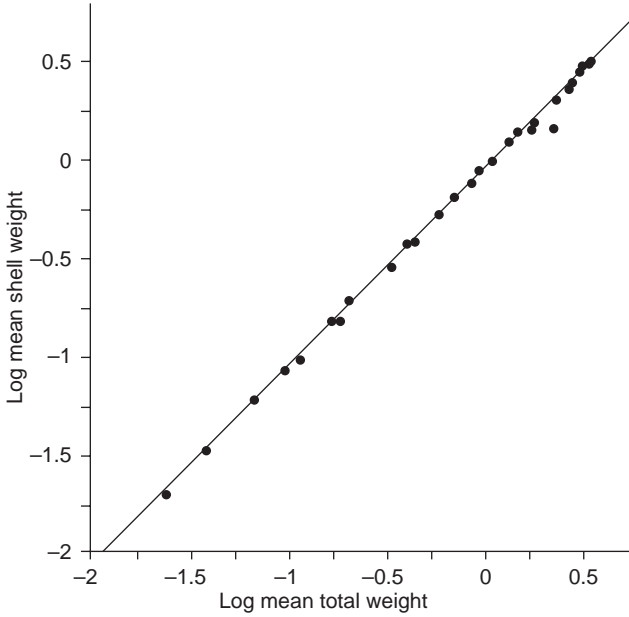
## DISCUSSION

The most notable finding in the present study is that all three possible relationships between the proportion of shell mass and body size, i.e. positive, negative and none, were recognized among molluscan species

inhabiting the same shore environment. This indicates that in some species the proportion of shell mass increased with body size, while in others it either decreased or showed no change with size.

Amongst various functions that shells may play, defence against predators is considered the most important from an evolutionary point of view (Vermeij, 1987). In intertidal and shallow marine environments, there are many potential predators such as fish and decapod crabs that either crush or break molluscan shells. Shell mass is a relevant factor as it is known that the mechanical strength of a shell is closely related to its mass (Currey, 1988). Therefore, if shell mass increases in proportion to body size, the larger the molluscan individuals the more resistant they are to shell breakage by predators. This relates closely to the phenomenon of 'size refuges' (Paine, 1976; Boulding, 1984; Jeffries & Lawton, 1984; Lawton & Hughes, 1985) whereby prey can escape predation because of their size. It is interesting to observe that there were more species demonstrating an increasing proportion of shell mass with body size than those demonstrating a decreasing proportion. Thus, the majority of taxa had either a proportional or an over-proportional increase in shell weight with increasing body size, suggesting that the shells of these taxa are more resistant to breakage as they attain larger sizes.

There were also taxa (nearly a quarter of all



**Fig. 5.** Relationship between log mean shell weight and log mean total weight derived from the 10 largest individuals of each species.  $y = -0.0597 + 1.009x$ ,  $r^2 = 0.997$ .

examined) that had a decreasing proportion of shell mass with body size. This, however, does not indicate that these taxa have weaker shells as they grow. As the magnitude of decline in percentage shell weight is small (no more than 10% decline from small to large individuals), overall shell strength is still expected to increase rather than to decline with increasing body size.

When considering defence against predators such as crabs that fracture or chip away part of a shell and also gastropod predators that make a hole through the shell (e.g. *Morula* and *Ergalatax* in the study site), the relative strength of shell ( $F_s$ ) can be expressed as a function of shell mass per unit surface area of soft tissue:

$$F_s = r W_s / W_f^{2/3} \quad (5)$$

where  $r$  is a species-specific constant. Assuming that tissue weight can be expressed as a fraction of shell weight, i.e.  $W_f = cW_s$  ( $0 < c < 1$ ), thus:

$$F_s = r W_s / W_f^{2/3} = r W_s / (cW_s)^{2/3} = r' W_s^{1/3}$$

This suggests that  $F_s$  scales roughly with one-third power of shell mass, or simply, shell length (or thickness), in so far as the ratio of shell weight to tissue weight remains constant; this is in conformity with some empirical studies (Currey & Hughes, 1982; Cook, Currey & Sarsam, 1986; Cook & Kenyon, 1993; Lowell *et al.*, 1994). For example, a mollusc with a shell length of 30 mm will have a 10 times stronger shell than an individual with a 3 mm-long shell. Note that 'compression' resistance or strength which is often measured in the laboratory may not be directly relevant to intertidal molluscs which do not generally experience heavy predation pressure from predators (e.g. fish) that crush the entire shell. In theory 'compression' strength will

depart more from 'chipping' strength as shell size increases, if the former scales with the square of a length measurement.

If we assume that a 10 times increase in one dimension of a mollusc is accompanied by a decline in the percentage shell mass from 75 to 60%, according to eqn (5) the initial shell strength is:

$$\text{initial } F_s = r W_s / W_f^{2/3} = r (0.75/0.25) W_f / W_f^{2/3} = 3 r W_f^{1/3}$$

and the terminal shell strength can be derived by substituting  $W_f' = 1000 W_f$  and  $W_s' = (0.6/0.4) W_f'$ , thus:

$$\text{terminal } F_s = r W_s' / W_f'^{2/3} = r (0.6/0.4) W_f'^{1/3} = 15 r W_f^{1/3}$$

Therefore, even with this magnitude of decline in the proportion of shell mass, the terminal shell strength is five times the initial value (if we assume compression strength, this would be 25 times). Apparently the observed magnitude of decline in the proportion of shell mass is not large enough to lead to weakening of shell strength. In general terms, if a mollusc increases  $m$  times in length dimension and the proportion of its shell mass changes from  $p_1$  to  $p_2$  ( $0 < p_1, p_2 < 1.0$ ), according to eqn (5) the terminal shell strength is calculated to be

$$t = m \frac{p_2(1-p_1)}{p_1(1-p_2)}$$

times as large as the initial strength. For the range of values of  $p_1, p_2$  and  $m$  encountered in the present study,  $t$  is always larger than unity, so shell strength increases with body size. Therefore, these taxa with decreasing proportion of shell mass with body size can nevertheless maintain sufficient shell strength, while any saving made in terms of reduced investment into the shell can be channelled to reproduction, thus improving potential reproductive success.

Our analysis indicates that the magnitude of change in the proportion of shell mass ( $P_s$ ) with body size, the slope  $\beta$  in the regression eqn (3), is related to the values of  $P_s$  in small individuals. Species with relatively high  $P_s$  in small individuals tend to have low values of  $\beta$ , while those with low  $P_s$  in small individuals tend to have high values of  $\beta$ . Thus, as two extreme cases, species can either (1) make a larger investment in shells early in the life cycle and gradually reduce the proportional contribution as individuals grow, or (2) make a limited shell investment at first and then increases its magnitude as they grow. Overall, the data suggest that the second strategy is more widely adopted by the molluscan species under study. While there may be certain advantages in making an extra investment in shells when individuals are small, particularly to increase the survivorship of small-sized individuals which are vulnerable to various mortality factors, there may exist physiological constraints to the level of investment that small individuals could achieve. For example, small individuals may have a far less efficient metabolism for producing the organic material which is needed for shell production compared with larger individuals.

Apart from defence against potential predators and

physical damage, shells of intertidal molluscs are thought to be important for preventing desiccation (McQuaid, 1996). Thus, it may seem reasonable that those taxa which occurred in the upper intertidal tended to have a higher proportion of mass being invested in protective shells. In theory, the effectiveness of a shell as a cover for preventing water loss will depend more on its material quality than on its sheer mass. This means that, within a species, shell mass will only have to increase in proportion to the surface area of body mass to fulfil its role as a cover, in so far as shell shape is unchanged, so, the proportion of shell mass will decrease with body size. Thus, predation and desiccation risks could exert slightly different effects on shell morphometry.

Therefore, interspecific variation in the ontogenetic patterns of relative investment in shell and non-shell parts among intertidal molluscs is considered to result from a combination of factors including predation, desiccation and trade-offs with other physical/physiological characteristics, the relative effects of which must have varied for different taxa over evolutionary time. Simultaneous operation of opposing influences would make the elucidation of causal relations very difficult in comparative studies of morphometry. Unfortunately, relevant information, particularly of an evolutionary nature, is scarce and further study will be needed to throw more light on the ecological and evolutionary background of morphometric variation in molluscs.

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